THE BEHAVIOR AND HABITS OF THE MYRMECOPHILOUS SCARAB CREMASTOCHEILUS STATHAMAE CAZIER WITH NOTES ON OTHER SPECIES (COLEOPTERA: SCARABAEIDAE)

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Received for Publication August 20, 1961

ABSTRACT

A list of all the known host ants and beetle species (Cremastocheilini) is given along with a detailed description of the behavior and habits of *C. stathamae* with the honey ant *Myrmecocystus mimicus*. Information on the feeding habits and behavior of the ant are included. It is determined that the true relationship between the species of the genus *Cremastocheilus* and their host ant species is not yet known and that these beetles are found associated with at least 11 different genera of ants.

Aside from isolated collecting records and brief observations involving only a few specimens of *Cremastocheilus* little is actually known about the behavior of these myrmecophilous beetles or of the intricacies of their relationship with the associated ant species. Wheeler (1908) summarized most if not all of the information available at that time on their behavior and drew several conclusions that do not appear to be entirely in accord with observations made subsequent to his publication. This is not too surprising as Wheeler had only a limited number of published accounts to draw upon and without exception all of them gave only fragmentary and often questionable information. Wheeler's own experiments are not conclusive primarily because of the difficulty in observing the behavior of the beetle underground or in an artificial ant nest.

Brief observations have been made on the occurrence of these beetles with various species of ants on the surface of the ground

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near to or away from the opening to the nests and in the upper galleries of the nest itself. Wheeler introduced several species of *Cremastocheilus* into artificial nests of several species of ants and obtained some interesting behavior information which in part led him to conclude that "the Cremastochili are not true guests, or symphiles, as Wasmann supposed (1894), but persecuted intruders (Synechthrans) that may eventually become indifferently tolerated guests (synoëketes)." There is still too little information available to either verify or disprove this conclusion. However, the observations made on *Cremastocheilus stathamae* Cazier and its behavior in relation to *Myrmecocystis mimicus* Wheeler outside the nest, indicate that in some activities they could be classified as a synechthrans (unwelcome guests), synoëketes (unnoticed or tolerated guests) or as Symphiles (true guests).

Ayre (1958) observing the behavior between adults of *Cremastocheilus armatus* Walker and *Formica integroides subnitens* Creighton suggests that the beetle is a persecuted synoëkete (synechthran). Howden (in lit.) also working in British Columbia on *Cremastocheilus armatus* Walker but in the nest of *Formica subpolita camponoticeps* Wheeler reports that one of two adults taken from the nest was feeding on an ant larvae. This behavior might indicate either a synechthran or symphile relationship with this species of ant. Limited observations made by Cazier (1961) on the behavior of the adults of *Cremastocheilus mentalis Cazier* and the ants *Dorymymex pyramicus* (Roger), *Novomessor albisetosus* (Mayr), *Pogonomyrmex maricopa* Wheeler and *P. barbatus* (F. Smith) would indicate symphile relationships at least in part. *Dorymyrmex pyramicus* (Roger) at a different location apparently has no relationship with *Cremastocheilus stathamae* Cazier although both are abundant in the area.

Field observations made by the authors in several localities indicate the existence of differences in behavior on the part of various species of *Cremastocheilus* and in the species of ants in a single location or between different locations. These differences could easily account for the varied and sometimes apparently contradictory reports that have been published on behavior or relationships. It is also possible, and we think probable, that the species of *Cremastocheilus* are at different evolutionary levels in their development from being unwelcome guests (Synechthrans) to true guests (Symphiles) and that we may yet discover species that are true symbionts. To date little or nothing has been done to study the relationship between the beetle (adults and immature stages) and the ants inside of the colony proper.

As a result of new information it is apparent that Wheeler's (1908, p. 70) statement is at least partly incorrect, "These records show that in the great majority of cases the hosts of *Cremastochilus* belong to the genus *Formica*. Although *C. spinifer* has been taken with *Pheidole, C. variolosus* with *Aphaenogaster* and *C. squamulosus* with a species of *Campanotus*, it is practically certain that these are accidental or irregular associations." We now know that *Cremastocheilus* species are regularly associated with the following ten genera of ants: *Formica, Polyergus, Camponotus, Aphaenogaster, Veromessor, Pheidole, Myrmecocystis, Novomessor, Popononyrmex* and *Dorymyrmex.* The closely related Scarab *Genuchinus ineptus* (Horn) has been found with ants belonging to the genera *Formica, Liometopum* and *Crematogaster.* That the distribution of *Cremastocheilus* conforms closely with that of *Formica* and that they occur more often with species belonging to that genus seems inevitable. According to Creighton (1950, p. 450) the genus *Formica* is the largest genus in North America and its species constitute approximately one-sixth of our entire ant fauna. It occurs throughout the United States, most of southern Canada, and in sections of Mexico.

Table one is a compilation of the known records. The names of the host ants have been changed in many cases to conform to the nomenclature and status established by Creighton (1950).

The authors wish to express their gratitude to Dr. E. Gorton Linsley for the assistance rendered in this study. It was he who first took notes on the beetles' behavior and realized the potentialities of the find even before the size of the population had been determined. We would also like to thank Dr. and Mrs. Alexander B. Klots for finding and keeping track of several specimens on the first day of study and Dr. Henry Howden who supplied information from his own collecting experiences and from the Canadian National Collection. We wish to express our appreciation to Dr. William S. Creighton who made the determinations on the ant species collected in the study plot and to

Table 1

Cremastocheilus species	Host ant species	Locality	Authority
castanea Koch	*Formica fusca* Linné	North Carolina	Beutenmuller
		New York	Wheeler
	Formica schaufussi Mayr	New Jersey	Davis & Wheeler
		Washington, D. C.	Pergande
		New York	Wheeler
	Formica exsectoides Forel	New Jersey	Davis & Wheeler
	Formica exsectoides Forel	Washington, D. C.	Schwarz
	Polyergus lucidus Mayr with *Formica pallidefulva nitidiventris* Emery as slaves	New York	Wheeler
	Formica fusca Linné	Colorado	Schmitt
	Formica fusca Linné	Kansas	Howden, in lit.
canaliculatus Kirby	*Formica schaufussi* Mayr with *F. fusca Linné* as slaves	New Jersey	Davis & Wheeler
	Formica rubicunda Emery with *F. fusca* Linné as slaves	New Jersey	Davis & Wheeler
	Formica exsectoides Forel	New Jersey	Davis
	Formica fusca Linné	Massachusetts	Morse
	Formica fusca Linné	New Hampshire	Howden, in lit.
		Massachusetts	Howden, in lit.
	Polyergus rufescens bicolor Wasmann with *Formica fusca* Linné as slaves	Ontario	Howden, in lit.
	Camponotus pennsylvanicus (DeGeer)	Pennsylvania	Hamilton
mexicanus Schaum	*Formica rufibarbis* gnava Buckley	Arizona	Schaeffer
	Formica obscuripes Forel	Arizona	Wenzel
schaumi LeConte	*Veromessor andrei* (Mayr)	California	Mann
variolosus Kirby	*Aphaenogaster fulva* Roger		Schwarz
squamulosus LeConte	*Camponotus* (*esuriens*) probably *C. abdominalis* Fabricius or *C. vicinus* Mayr	Georgia Florida	Schwarz
crinitus LeConte	*Formica rufibarbis gnava* Buckley	Texas	Wheeler
retractus LeConte	*Formica rufibarbis gnava* Buckley	Texas	Wheeler
	Formica ciliata Mayr	Colorado	Wheeler
harrisi Kirby	*Formica schaufussi* Mayr	North Carolina	Wheeler
	Formica subintegra Emery with *F. schaufussi* Mayr slaves	New Jersey	Wheeler
armatus Walker	*Formica subpolita camponoticeps* Wheeler	British Columbia	Howden, in lit.
	Formica integroides subnitens Creighton	British Columbia	Ayre
	Veromessor andrei (Mayr)		Essig

Table 1—(Continued)

Cremastocheilus species	Host ant species	Locality	Authority
pilisicollis Horn	*Veromessor andrei* (Mayr)	California	Mann
	Formica obscuripes Forel	California	Mann
spinifer (Horn)	*Pheidole desertorum* Wheeler	Texas	Wheeler
wheeleri LeConte	*Formica oreas* Wheeler	Colorado	Wheeler
	Formica criniventris Wheeler	Colorado	
	Formica microgyna Wheeler	Colorado	
	Formica rasilis Wheeler	Colorado	
	Formica ciliata Mayr	Colorado	
	Formica exsectoides Forel	Colorado	Wheeler
	Formica obscuripes Forel	Colorado	
		Manitoba	Howden, in lit.
planatus LeConte	*Formica obscuripes* Forel	Arizona	Wheeler
	Camponotus maccooki Forel	California	Mann
	Formica rufibarbis occidua Wheeler	California	Mann
planipes (Horn)	*Formica obscuripes* Forel	Arizona	Wheeler
opaculus (Horn)	*Formica obscuripes* Forel	Arizona	Wheeler
stathamae Cazier	*Myrmecocystis mimicus* Wheeler	Arizona	New Record
	Novomessor cockerelli (E. André)	Arizona	New Record
mentalis Cazier	*Novomessor albisetosus* (Mayr)	Arizona	Cazier
	Pogonomyrmex maricopa Wheeler	Arizona	Cazier
	Pogonomyrmex barbatus (F. Smith)	Arizona	Cazier
	Dorymyrmex pyramicus (Roger)	Arizona	Cazier
beameri Cazier	*Pogonomyrmex barbatus* (F. Smith)?	Arizona	Cazier
lengi Cazier	*Myrmecocystis mimicus* Wheeler?	Arizona	Cazier
constricticollis Cazier	*Myrmecocystis mimicus* Wheeler	Arizona	Cazier
	Pogonomyrmex barbatus (F. Smith)?	Arizona	Cazier
Genuchinus ineptus Horn	*Formica obscuripes* Forel	Arizona	Wenzel
	Crematogaster coarctata Mayr	Arizona	Cazier
	Liometopum occidentale luctuosum Wheeler	Arizona	New Record

Phil Bagwell we extend our thanks for allowing us to dig holes on his property, stake out the plot and leave our markers in place indefinitely. Without such generous cooperation studies such as this one would of course be impossible.

The paucity of behavior and biological information in the genus *Cremastocheilus* is especially evident in the *Trinodia* section which are relatively uncommon in collections. With one known exception, no species in this section of the genus have previously been found in sufficient numbers in any one locality with their ant hosts to allow for a detailed study. In 1958 the senior author located a large population of *C. mentalis* Cazier associated with 4 species of ants (Cazier, 1961) but was unable to spend sufficient time in the area to get much information. A return trip to the locality was planned for 1959 but before this was accomplished the large population of *C. stathamae* Cazier was found conveniently located only 7.5 miles from the Southwestern Research Station near Portal, Arizona. In spite of a heavy population of punkies co-inhabiting the area, the ants and the *Cremastocheilus* were observed every day for 42 consecutive days for their entire active period during each day. The plot was further checked occasionally in 1960 and 1961 and the activity and behavior appeared to be the same as that observed in 1959 and the beetles just as abundant.

The first specimen of *C. stathamae* Cazier was collected on August 2, 1959 in a narrow, dry, sandy wash as it was being pulled by a single ant (*Myrmecocystis mimicus* Wheeler) toward the entrance to its nest. The ant was allowed to take the beetle for about 2 feet and get it inside the nest turret before the specimen was collected. A search of the area on the same day by Dr. E. G. Linsley and the authors produced 6 males and 18 females. On August 3, 14 males, 13 females; August 4, 2 males, 2 females; August 5, 1 male, 4 females; August 6, 1 male, 1 female; and on August 7, 4 males, 8 females. On August 8 we stopped killing the specimens, staked out the ant nests, started marking the beetles and continued making detailed observations.

The area in which these observations were made is located 2.5 miles northeast of Portal, Arizona, on the road to San Simon at an elevation of about 4700 feet. The study plot, which was located about 200 feet east of the road, extended for about 246 yards east and west by 204 yards north to south. It was situated on an aluvial fan formed by a small wash which was usually dry but evidently carries considerable water during the rainy season. The drainage is from the foothills of the Chiricahua Mountains. The surface covering consisted primarily of silt, sand and soil in a layer of from 0 to 12 inches, underlaid with caliche. The southwest corner of the plot was somewhat rocky, especially in the

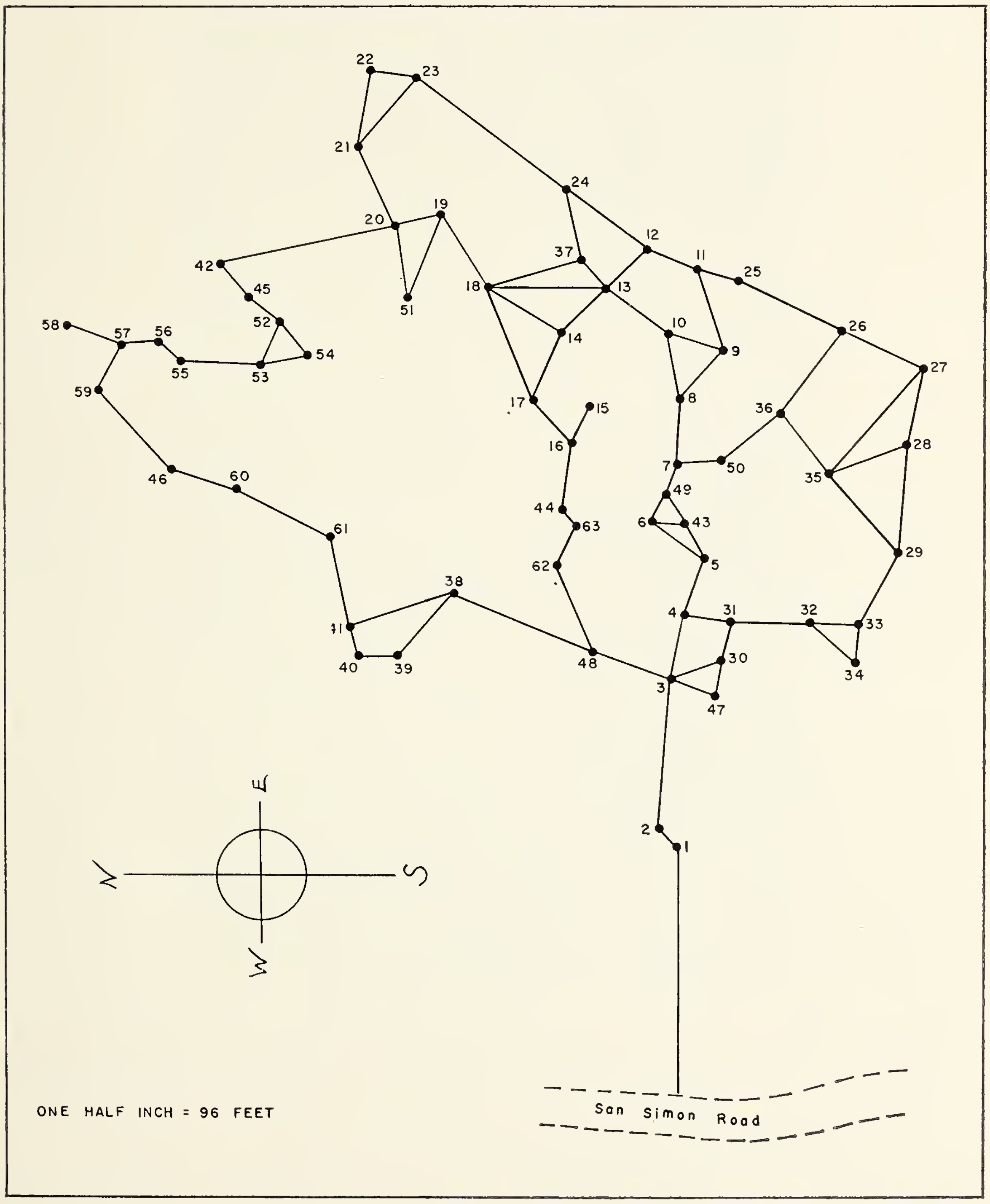

FIG. 1. Map of study plot showing relative location of the *M. mimicus* nests.

vicinity of the main wash, and the entire plot was traversed by small, shallow, sandy side washes.

The principal vegetation cover consisted of tar-bush, *Flourensia cernua* D.C. which is a small shrub with a hoplike odor, bitter taste and is unpalatable to livestock. In the northern half of the plot the tar-bush was mixed with an open stand of Creosote-bush, *Larrea tridentata* (D.C.), which also has a strong characteristic odor and is seldom eaten by livestock. The predominance of these two plants was probably the reason why we were not bothered by cattle feeding on this open range. There were scattered plants of *Yucca elata* Engelman, Mesquite, *Prosopis juliflora* (Swartz) D.C. and a sparse assortment of grasses and composites. Most of the ground between the primary plant shrubs was clear of vegetation cover and this is where the majority of the *M. mimicus* Wheeler ant colonies were located.

On August 8 discarded pieces of molding, 3–6 feet long were taken to the plot to serve as stakes and old pieces of white cloth to serve as flags. A stake was placed in the tar-bush nearest each ant colony that had been observed from August 2–7 inclusive and then other colonies in the area were given the same treatment until a total of 63 were marked. Late in September it was discovered that there were about 30 additional colonies that had either been missed or were new ones. Each stake had a white strip of cloth tied on top and each was given a number. Ten small bottles of paint were part of the equipment with which to mark the beetles and the stakes. The paint used was Testors Dope, a model airplane paint, that dries very rapidly, has good lasting qualities and apparently does not harm the beetle if kept on the elytra. The presence of the paint spots on the beetles did not appear to disturb the ants. Three test spots of different colors painted on a small pebble at the entrance to nest number 13 in August of 1959 were just as bright as ever in April, 1961 in spite of the ants and the heavy winter rains and winds that occurred in the area. As the beetles were marked, the same color combinations were put on the stakes with an 0 to indicate that the beetle was being taken out of the nest and an X if he were being taken into the ant colony. This information was also recorded in notebooks along with other observations. To avoid any confusion that might result in distinguishing shades of colors, 10 of the most distinct were used as follows: white, pale yellow, dark yellow, green gold, silver, pale blue, dark blue, orange and red. The first 10 beetles marked were given single spots of color on the right elytron, right being as the beetle faced away from the marker, and all subsequent markings involved different combinations of colors using both elytra. A total of 51 beetles were marked with different combinations and released.

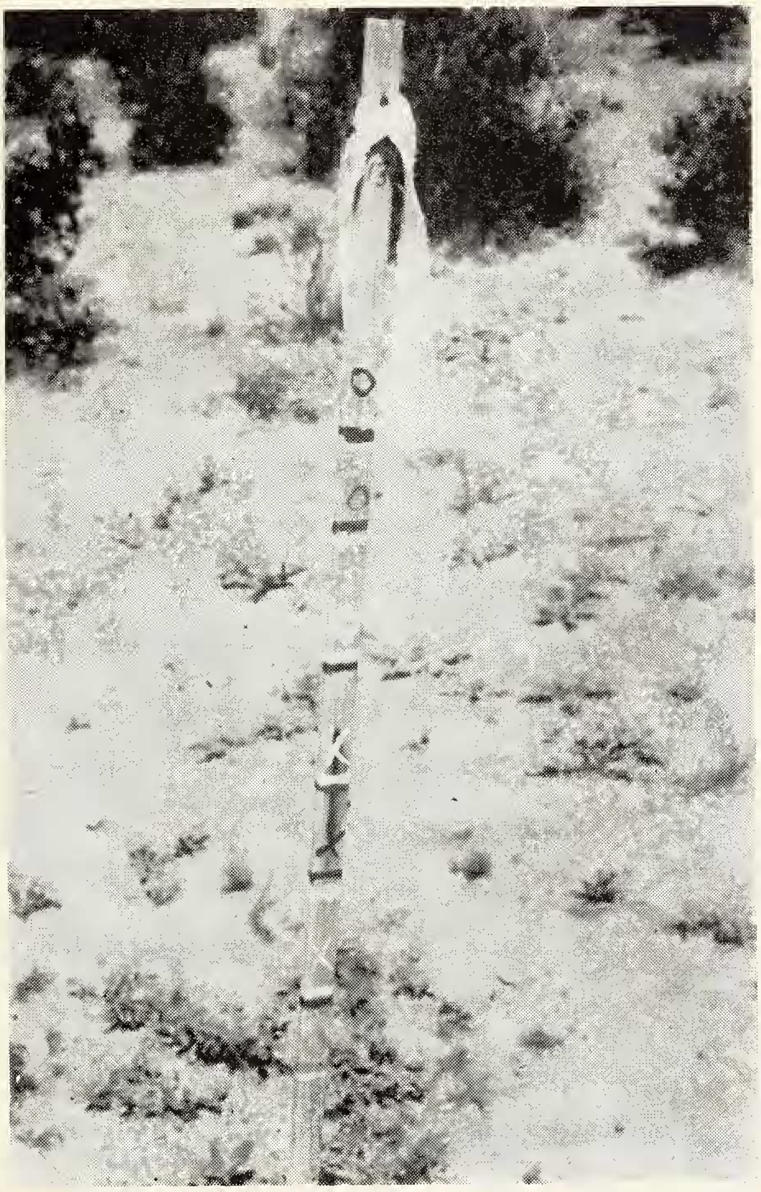

Fig. 2. Stake marking nest no. 13 showing the method of indicating the number of beetles being brought into or out of the nest and the color combinations used on each.

It was soon evident that beetle activity was in large part dependent on the activities of the ants which in turn were definitely adjusted to the climatic factors of sunlight, temperature, moisture and wind. Also, raiding columns of *Dorymyrmex pyramicus*

(Roger) would rather completely change the behavior pattern of a colony of *M. mimicus* Wheeler. The close relationship between the ants and the beetles necessitated the careful observation of both. One of the most interesting and characteristic features of the genus *Myrmecocystus* (Honey ants) is that in at least some species certain members of the colony are converted into living bags of honey called repletes (Creighton, 1950, p. 437). *M. mimicus* Wheeler was one of the species in which repletes were unknown, which caused Wheeler to create some systematic confusion (Creighton, 1950, p. 448). Exploratory excavations of three *M. mimicus* Wheeler colonies on the plot proved without doubt that they do produce repletes at least in this location. In the first colony they were found in chambers at about 3 feet from the surface, in the second at about 3 and ½ feet and in the third at slightly over 4 feet. These excavations were made in an attempt to get information on the beetles behavior below ground but the only information gained was that one specimen was taken from the first nest at about 14 inches from the surface. Additional studies are planned to secure information on the beetles behavior and biology within the colony. All three of the excavations were filled in with loose dirt and all three colonies were active again on the surface within about a week. On September 1 the second colony, excavated sometime between August 5 and 10, brought out an unmarked beetle.

As mentioned, previously, most of the *M. mimicus* Wheeler colonies are located in the open areas between plants. Each nest is characterized by having a more or less rounded crater with variously shaped holes in the center. The craters are made up of small or medium sized pebbles and soil, surrounded on the outside by discarded pieces of plants, insects and other debris. Measurements on the hole diameters were made on 42 colonies taken at random with the following results:

	19 asymetrical holes		23 symetrical holes	
	East-West	North-South	East-West	North-South
average	1.30 inches	.92 inches	.92 inches	.84 inches

These figures indicate a slight correlation between size of hole and exposure. The east-west measurements in both cases are larger which means a longer exposure to sunlight. In 10 measurable turrets surrounding asymetrical holes the average diameter was 7.17 inches, in 17 symetrical holes the average diameter was 6.22 or almost an inch smaller. The measurements were made to the outside of the crater limits. In only two or three instances were there 2 entrances to a single ant colony and these were close together, within 2–7 inches of each other.

Because of the density of the *M. mimicus* Wheeler colonies in the study area the distances between the colonies were measured to determine any spatial or territorial relationships that might exist. The minimum measurement was 14 feet between colonies 1 and 2 with an intervening small wash. The next closest colonies 6 and 49, were 18 feet apart with no intervening wash. The maximum distance was 132 feet separating colonies 23 and and 24 and the average distance between colonies was 49 feet. There seems to be no set spatial requirements for this spcies of ant and no readily observable factors that might have determined the location of the nests.

Several factors affected the behavior of *M. mimicus* Wheeler so that no beetles were being brought into or out of their nests:

1. Rain and cool weather usually either stopped ant activity altogether or confined it to bringing debris out of the nest and depositing it on the sides of the crater.
2. Raids by *Dorymyrmex pyramicus* (Roger) would stop all outside activity and the *M. mimicus* Wheeler workers would stay inside the nest entrance or occasionally bring a piece of debris out onto the side of the crater and then quickly retreat inside again.
3. Winds strong enough to carry sand or debris along the surface of the ground would keep the ants busy carrying these materials out for deposition on the crater walls.
4. Rains that carried materials into the nest opening would also cause these "clean out" activities.
5. Excessive heat would stop all outside activities even those involving "clean out".

On hot sunny days it was observed that if a shadow was over the nest entrance of an inactive ant colony for a few minutes the ants would become active and start foraging activities. On August 10 several cardboard boxes with two sides cut out were taken to the plot. At 9:30 A.M. a box was placed over colony number 3 which was inactive and at 9:42 A.M. they began bring-

Table 2

Date Aug.	Period of Beetle activity	Weather Conditions	Number of Beetles: IN-	Number of Beetles: OUT	Temperature (F.) and Rainfall recorded about 2 miles away: Rain	6 A.M.	12 Noon	6 P.M.	12 Mid.
2	11:30– 4:05	Warm, Sunny	4	10	Trace	68	93	80	78
3	9:15– 4:40	Rain night before, ground damp	6	7		78	98	90	80
4	9:05– 2:35	Cool, Sunny	1	1		72	72	82	75
5	9:05– 2:36	Partly cloudy	2	4		72	90	90	75
6	4:05– 4:25	Rain		2	1.00	73	90	80	74
7	9:55– 3:35	Very damp, sunny, occasional clouds, light breeze	3	9	.60	72	94	90	76
8	2:30– 3:30	Damp, cool	1	8		73	74	81	71
9	10:00– 1:45	Cloudy, threatened rain		1		71	95	75	70
10	9:42– 1:15	Hot, sunny	2	1		78	94	88	77
11	11:00– 2:40	Heavy rain night before, cloudy most of day	4	5	.30	74	80	80	73
12	10:03– 3:45	Scattered clouds, light showers, hot and humid	2	2	.10	73	94	90	78
13	11:30–11:55	Overcast, threatened rain, strong breeze, chilly	2	7		76	90	75	70
14	11:15–12:50	Mostly overcast, warm and humid		4		70	90	90	74
15	1:20– 3:15	Heavy rain night before, light rain in morning, overcast	1		.40	72	96	96	77
16	10:05– 1:00	Sunny in morning, overcast in afternoon	1	2		73	96	82	76
17	None	Sunny in morning, afternoon cloudy, strong breeze				74	96	83	73

ing a beetle out of the nest. However, he was not out by 12:10 P.M. so the box was taken off and at 2:05 P.M. they were successful in getting one out. A second box was placed over colony number 31 at 9:35 A.M. and they started foraging activities. At 9:45 A.M. they were bringing a beetle in from 15 feet away from the entrance. During these periods when the outside activities of the ants were limited there was no observed beetle activity either at the nest entrance or away from it. On one or two occasions, after ant activities had ceased for the day,

Table 2—(*continued*)

Date Aug.	Period of Beetle activity	Weather Conditions	Number of Beetles		Temperature (F.) and Rainfall recorded about 2 miles away				
			IN-	OUT	Rain	6 A.M.	12 Noon	6 P.M.	12 Mid.
18	10: 05	Sunny, occasional clouds, dry, strong breeze	1		.30	71	86	86	72
19	None	Cloudy, rain, cool			.20	70	84	75	70
20	None	Cool, overcast, light breeze				67	79	83	70
21	9: 50–12: 35	Rain night before, warm, some overcast		2		70	84	76	70
22	11: 20– 2: 50		2	2	.30	70	86	87	74
23	None	Sunny, scattered clouds, light breeze				71	91	—	—
24	2: 25	Rain night before, sunny, scattered clouds, strong breeze		1		—	—	—	—
25	None	Overcast, rain off and on				—	—	—	—
26	10: 30	Rain day before, morning hot, sunny		1		—	—	—	—
27–31	None								
Sept.									
1	9: 30	Clear, sunny, dry	1						
2–9	None	Sunny, breezy, very dry							
10	9: 45–10: 15	Rain night before, overcast, breezy	1						
11	9: 20–12: 40	Sunny, scattered clouds, light breeze	4						
12	10: 30– 1: 20	Sunny, breezy	1						

beetles were found sitting on the ground away from any nest apparently ''waiting'' to be picked up by the ants. They had probably been ejected from nests during the preceding active period and there hadn't been time for the ants to find them before one of the above listed factors stopped their foraging or swarming activities. No beetles were observed being ejected from the colonies when the ants were only engaged in ''clean out'' activities. If the beetles were considered by the ants to be foreign objects or used prey one would assume that this would be the time when most of the beetles would be expelled from the colonies. Apparently the ant is motivated by some other factors in the expulsion of the beetle or the colony has to be in a more excited state, as they seem to be during foraging or swarming.

Maximum periods of activity occurred in general when it had rained the night before and the temperature range was between 80° and 98° F. or on overcast days when rain was threatening but temperatures were high. During these periods the ants would send out directional foraging column's consisting of many individuals or single individuals would wander about in all directions. It was during the latter type that most if not all of the beetles were located and were being brought back to the nest. At the same time there would be considerable activity around the nest opening and beetles would be brought out. During the 42 days of observation on the plot the earliest ant and beetle activity started at 9:05 A.M. on August 4 and the latest activity occurred on August 6 with the capture of the last beetle at 4:25 P.M. The starting time and duration of activity was of course dependent on the various conditions previously mentioned.

Table two shows the time limits of beetle activity, the prevailing weather conditions during this period, the number of beetles being brought into and out of the ant nests and the rainfall and temperature according to date.

Of the 32 specimens of *C. stathamae* Cazier that were observed being brought into the nests by *M. mimicus* Wheeler only 4 of them involved more than one ant. In all other cases one ant would have its mandibles fastened to the upturned portion of the beetles clypeus and would either be leading it to the nest or on several occasions the beetle was between the ant and the nest walking or running backward or sideways. When 2 ants were involved, the second would usually have hold of a leg but would let go occasionally and sometimes leave. When one ant was involved the route followed to the nest was fairly direct, but when a second ant interfered the route was more erratic. The distances involved varied from 1 to 20 feet and if no obstacles were encountered they traveled at a rate of about 1 foot a minute. In one case it took an ant only 20 minutes to bring a beetle 18 feet to the nest through rocky ground. With few exceptions the beetles helped in getting to the nest as can be deduced by the short travel time involved and the fact that a single ant could not move a beetle unless assisted since the beetles by bulk are about 10–15 times the size of the ant. In another case a beetle was always in front of the ant while they traveled 15 feet to the nest. Eight ants from a colony, that was later excavated, brought a beetle out of their nest, dragged it 5 feet away at which point all the ants released their holds and some started back toward the nest. The beetle upon being released went straight back into the nest unassisted, getting there ahead of the ants who had pulled it out.

Unlike several other species that have been reported on in the past *C. stathamae* Cazier apparently does not fly directly into the immediate vicinity of the ant nest and those being brought in were observed from 4 or more feet away from the nest. Even those at 4 feet may have been individuals ejected from the nest and taken away to that distance by the ants before being released.

During the period when these observations were made the ants were carrying primarily animal booty back to the nest. None were seen feeding on or gathering pollen, nectar, or honeydew. Random samples of this booty contained the following:

Hymenoptera
- Remains of several wasps.
- Whole but dead *Novomessor cockerelli.*
- One live bee.

Orthoptera
- Several grasshopper nymphs.
- Grasshopper abdomen full of eggs.

Neuroptera
- Pieces of Myrmelionid adults.

Hemiptera
- Numerous whole, dead and alive, Cydnidae.
- Pentatomidae, whole.
- Phymatidae, whole.

Lepidoptera
- Moth adults, pupae and larvae.

Coleoptera
- Curculionidae, dead and alive.
- Scarabaeidae, dead and alive.
- Tenebrionidae, dead and alive.
- Coccinellidae, dead.
- Buprestidae, dead.
- Meloidae, dead.
- Alleculidae, dead.

Diptera
- Pupa

Phalangida
- Pieces and whole dead ones.

There were also occasional pieces of feathers, seeds, leaves and flowers

These booty samples would seem to lend support to the explanation that the *Cremastocheilus* are brought in as food during normal foraging activities. This may in part be the case but such a simple explanation leaves unanswered a number of questions that enter into the relationship. 1. Other live booty being brought in offers resistance and more than one ant is usually involved in getting it to the nest. 2. The *Cremastocheilus* usually offers no resistance and on numerous occasions seems to be pulling the ant toward the nest, the ant serving as a sort of rudder. 3. Only one ant usually takes the *Cremastocheilus* to the nest and where two ants become involved progress is actually

Fig. 3. Adult *C. stathamae* being pulled toward a nest by two workers of *M. mimicus*.

impeded. 4. Some of the pieces and occasionally whole dead specimens of other booty end up around the outside of the crater. 5. No parts or whole dead specimens of *Cremastocheilus* are to be found scattered outside the nest entrance. 6. The only living things observed being brought out of the ant nest and "purposely" released is the *Cremastocheilus*. The beetles are found during normal foraging activities for prey but at this point the ant makes no attempt to kill, mutilate or eat the specimen as it does with other live booty. It assumes the role of host and guide to the nest.

In October and November of 1960, on a study plot located a half mile away, these ants were feeding on or gathering the pollen and nectar from at least two plants, *Parthenium incanum* H.B.K. and *Euphorbia albomarginata* Englm. and may have been getting honey-dew from a species of Aphid which is abundant on the underside of the leaves of the latter plant. During August and September they were observed on many

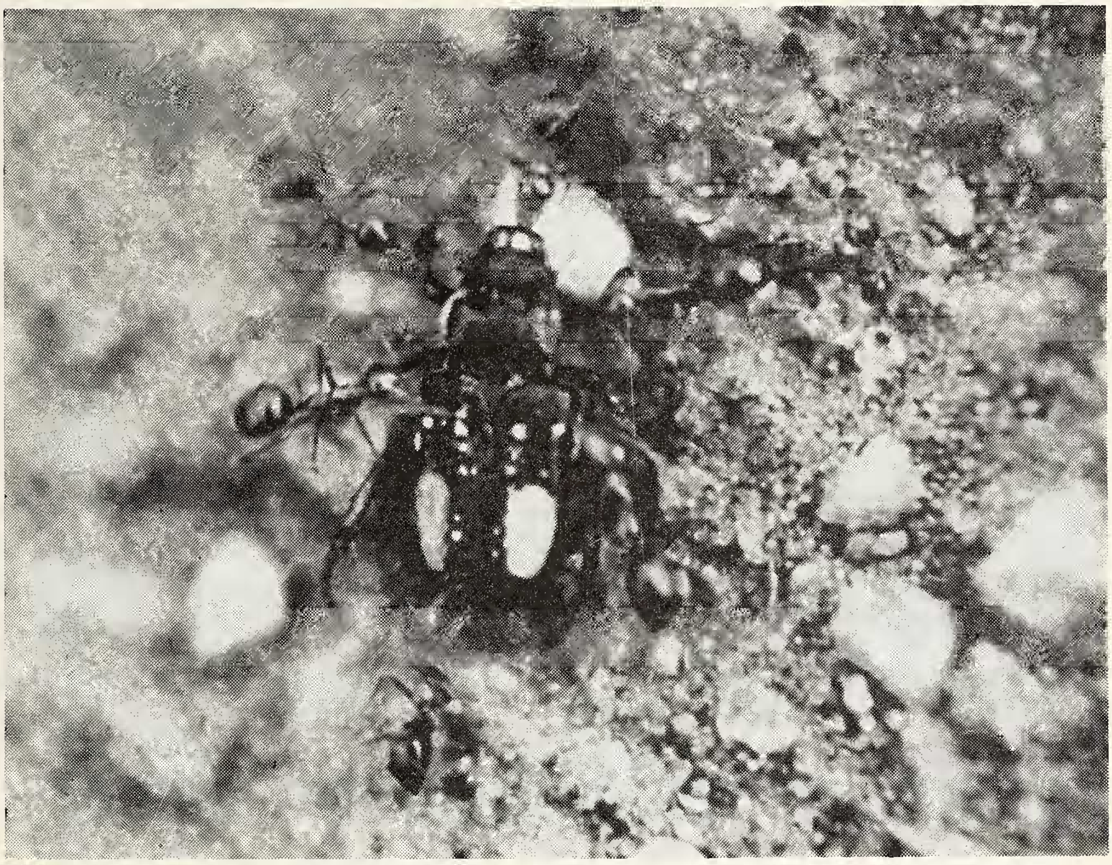

Fig. 4. Marked adult of *C. stathamae* being ejected from the nest by 6 workers of *M. mimicus.*

occasions carrying animal booty and were not found on flowers even though the above plants and *Zinnia pumila* Gray, *Baileya multiradiata* Harv., *Verbesina encelioides* (Cav.), *Gutierrezia microcephala* (D.C.) and *Orobanche fasciculata* var. *lutea* (Parry) were abundant and in full bloom around the nests. It may be that in late fall the ants fill the repletes with nectar and honey-dew as a winter supply of food or they might be filling a newly developed batch of repletes for this purpose. The repletes present in the colonies excavated in August of 1959 were full even though the ants were apparently gathering on.y animal booty at that time.

A total of 76 beetles were observed being brought out of the nests by the ants and the behavior pattern of the beetle toward the ants is in contrast to that exhibited when it is being brought in. Also many things happen to amuse the observer and the behavior is more complicated. In most of the nests it was possible to look into the opening for an inch or two and occasionally see a group of ants attached to the legs of a beetle working it upward toward the nest entrance. This often took considerable time and the efforts of from 6 to 8 ants on the average. The beetle would either hold onto the sides of the burrow with the legs that were not being held by ants, wedge itself into cracks or under small projections or try to get further back down into the nest. Once the ants were successful in getting the beetle out of the hole and over the crest of the crater they would drag it for from 1 to 9 feet from the nest but usually only 4 or 5 feet. As progress was made away from the nest the ants would drop off one or two at a time until the beetle was left alone. When the distances were long and the ants attached few, the beetle would assist by walking, once they were away from the immediate vicinity of the nest. When the beetle was deserted by the ants its usual reaction was to fly but there were variations in this behavior as can be seen from the following descriptions.

On August 2 at 3:40 P.M. a beetle was pulled out of a colony by 6–8 ants, one on the clypeus and the rest on the legs. It was about 5 and a half feet from the nest where all but one ant deserted, whereupon the beetle dragged the single ant back into the nest.

On August 4 at 2:35 P.M. 7–8 ants brought a beetle out of their colony and left it about a foot from the nest. The beetle walked away another 2 feet where it was picked up by the large *Novomessor cockerelli* (E. Andre) that started off toward its nest. Within a few feet the *N. cockerelli* (E. Andre) tried tc cross a column of *Dorymyrmex pyramicus* (Roger) and was attacked. It dropped the beetle which walked about 2 inches and flew. The *N. cockerelli* (E. Andre) succumbed to the attack of the *D. pyramicus* (Roger) as they were seen to do on several other occasions even though the latter ant is much smaller.

On August 12 at 1:10 P.M. 5 ants brought a beetle out of colony number 3 and took it 3 feet away where 2 different ants found it and took it back into the same ant colony at 1:19 P.M.

On August 2 at 2:19 P.M. a beetle was observed being pulled out of a nest by 6 or 8 ants that would repeatedly get him out 1 or 2 inches only to have it go back in.

On August 9 at 10:00 A.M. several ants brought a beetle out and before 3 of them could let go of its legs the beetle flew away with them.

On August 10 at 9:45 A.M. a single ant was bringing in a beetle from 15 feet away. They arrived at the nest at 9:49 A.M. where the beetle was given a silver spot before disappearing into the colony. At 10:09 A.M. it was being brought out again but managed to get back into the nest. Between 10:09 and 10:45 A.M. silver was brought out but got back in 8 times. Up to 12:10 P.M. it was still in the nest.

On August 11 colony number 13 brought beetles out at 11:20, 11:25 and 11:40 A.M. At 12:20 P.M. they were dragging an unmarked beetle toward the nest but after being marked it got away from the ants and flew. Also at 12:20 P.M. they were given a beetle that was found nearby and after taking it into the nest for a few minutes brought him out and it flew away.

On August 11 at 2:05 P.M. an ant from colony number 9 was found bringing in a beetle. It was in the colony only a few minutes when 6 or 8 ants brought it out and with its help took it about 5 feet from the colony where all the ants left it. A single ant, not one of the group that escorted it out, found it and with its help took it back into the colony. At 3:15 P.M. this same beetle was found on the ground about 100 feet from the colony.

Although as a general rule the beetles did not appear to want to leave the ant colony there were 2 or 3 cases where they actually helped the ants get them out and then flew at the earliest possible moment. On September 12 a female beetle came out of colony number 39 very rapidly and flew as soon as she was marked.

The concerted effort on the part of the ants to get the *Cremastocheilus* out of the nest and the beetles usual obvious reluctance at being ejected would lend support to Wheelers conclusion (1908, p. 75) that they are persecuted intruders (*Synechthrans*) that may eventually become indifferently tolerated guests (Synoeketes). The only other explanations that can be offered at the moment, without evidence to support them, is that the ants

Table 3

Ant Colony number	*Beetle brought in*	*Beetle brought out*	*Markings*	
			Left Elytron	*Right Elytron*
3		Aug. 10		Dark blue
		Aug. 12	Pale blue	White
		Sept. 11	White	Dark yellow
4		Aug. 12	Orange	Pale blue
5	Aug. 22		Orange	Dark blue
6		Aug. 8		Pale blue
		Aug. 13	Pale blue	Gold
7		Aug. 9		Orange
		Aug. 11		Pale yellow
8		Aug. 14	Dark yellow	Pale blue
		Aug. 22	Orange	Pale yellow
9		Aug. 8		Green
	Aug. 11		White	Orange
	Aug. 11		White	Pale blue
10		Aug. 22	Orange	White
12		Aug. 14	Pale blue	Dark yellow
13		Aug. 11	Pale blue	Red
		Aug. 11	White	Green
		Aug. 11	Red	White
	Aug. 11		Green	White
	Aug. 11		White	Red
	Aug. 12		Green	Pale blue
		Aug. 14	Pale blue	Silver
15		Aug. 13	Pale blue	Dark blue
16		Aug. 13	Gold	Pale blue
17	Aug. 13		Pale blue	Pale blue
21		Aug. 11	Red	Pale blue
		Aug. 14	Silver	Pale blue
23	Aug. 18		Orange	White
		Sept. 11	White	Pale yellow
28		Aug. 8		Dark yellow
	Aug. 10			White
29	Aug. 15		Dark blue	Gold
30		Aug. 12	Pale blue	Green
31	Aug. 8			Red
	Aug. 10			Silver
32	Aug. 13		Dark blue	Pale blue
37		Sept. 1	Red	Dark yellow
		Sept. 10	Red	Orange
39	Aug. 12		Pale blue	Orange
		Sept. 12	Orange	Red
42		Aug. 16	Pale blue	Pale yellow
	Aug. 22		Pale yellow	Green
43	Aug. 16		Pale yellow	Pale blue
44		Aug. 16	Dark blue	White
		Aug. 24	Green	Pale yellow
		Aug. 26	Red	Pale yellow
45		Aug. 21	Red	Dark blue
46		Aug. 21	Orange	Green
56		Sept. 11	Red	Green
59		Sept. 11	White	White

eject the beetle during its breeding season or that the beetle becomes an obnoxious guest at some point in the development of the ant brood. Specimens of *C. knochi* LeConte were reported by Lugger (1891) as mating in an open field but to date we have been unable to observe any mating activity in *C. stathamae* Cazier in spite of their abundance. Horn (1871) reported finding *C. schaumi* LeConte and *C. angularis* LeConte apparently eating ant pupae and Howden (in lit.) has found *C. armatus* Walker feeding on ant larvae. Such activities might cause their expulsion by the ants.

Table 3 contains the number of the ant colony, the beetles and the dates on which they were being brought in or out of the ant colonies and the color markings given each specimen. It covers the dates between August 8 and September 12, 1959.

The primary purpose of marking individual beetles was to be able to trace the movements of each to see how far they traveled, whether or not they were confined to a single colony of ants, and to be sure the same individual wasn't being recorded many times. Unfortunately only 4 recoveries were made during the 42 days so the data is limited.

On August 11 at 2:05 P.M. at colony number 9 a beetle was marked white on the left and pale blue on the right elytron and at 3:15 P.M. the same day it was found on the ground about 100 feet from colony number 9.

On August 8 between 2:30 and 3:30 P.M. a beetle coming out of colony number 6 was marked pale blue on the right elytron. Seven days later on August 15 this same individual was being brought out of colony number 11 which is located some 174 feet from number 6.

On August 15 at 3:15 P.M. a female beetle was brought into colony number 29 during a nuptial flight of the ants. The specimen was marked dark blue on the left and gold on the right elytron. On the following day at 11:35 A.M. this female beetle was being brought out of colony number 11 which is about 294 feet from colony 29.

On September 10 a female beetle was brought out of colony number 37 at 10:15 A.M. and after being marked red on the left and orange on the right elytron was taken back into the colony. On the following day the same beetle was brought out of the colony at 12:40 P.M. and flew away going west.

From these limited observations it would seem that the beetles are not confined to any given colony of ants and they do travel considerable distances. The latter fact might in part be responsible for the poor recovery record. Also their flight is rapid and difficult to follow.

In order to insure the least amount of disturbance in marking the beetles the incoming specimens were allowed to get inside the crater before being picked up. They were replaced in the same spot. The outgoing beetles were allowed to go until deserted by the ants and were ready to fly. They were then picked up, marked, and replaced in the same spot.

C. stathamae Cazier is also associated with the ant *Novomessor cokerelli* (E. Andre) or at least individuals were picked up by these ants and taken to their colonies. However, it is doubtful that the behavior pattern is anything like that shown with *M. mimicus* Wheeler since *N. cockerelli* (E. Andre) is so large that a single ant can pick the beetle off the ground and carry it. On September 10 a *N. cockerelli* (E. Andre) carried a dead *C. stathamae* away from the vicinity of colony number 51 and went 28 yards in 15 minutes carrying the beetle upside down most of the way. On several occasions the very small ant *Forelius foetidus* (Buckley) was seen crawling over and around a *C. stathamae* Cazier that was not moving. On August 7 at 12:20 P.M. a beetle was being brought out of a *M. mimicus* Wheeler nest by 5 or 6 of these ants but there were also 2 *F. foetidus* (Buckley) next to the entrance hole seemingly trying to help.

In most of the published literature referring to members of the genus *Cremastocheilus* the statement is made that the ants keep the beetles captive in order to ''milk'' them of the fluids that exude from the pubescent glandular areas located beneath or at the front and hind angles of the pronotum. The beetles have such a structure that may be glandular and some specimens show signs of having the angles of the pronotum chewed upon, presumably by the ants in their attempts to get at the glands beneath. If such is the case then in *C. mentalis* Cazier and *C. stathamae* Cazier these ''milking'' activities must be confined entirely or in large part to behavior within the nest. In field observations involving over 70 specimens of each species no ants were observed to concentrate on these areas of the beetle and were trying primarily to get the beetle into or out of the nest. In

C. stathamae Cazier the beetles are certainly not held captive all the time since two-thirds of the behavior observations given above were made on specimens being ''forcibly'' ejected from the nests by the ants.

Although *C. stathamae* Cazier was the predominant species of *Cremastocheilus* in this area, specimens of 2 other species were taken; *C. lengi* Cazier and *C. constricticollis* Cazier. They are, however, distinct species. *C. lengi* Cazier is the only member of the genus having 4-segmented tarsi and *C. constricticollis* Cazier is the only species having the pronotum only slightly more than one-half as wide as the elytra. Both species were found in association with *Myrmecocystis mimicus* although none were observed being taken in or out of the nest in 1959.

The plot was checked the middle of February 1960 and occasionally thereafter but there was no ant activity until the early part of June. The junior author checked on them July 22 and found 2 males and 10 females being brought out of colonies between 9:55 A.M. and 1:20 P.M. All the beetles were unmarked and were from colonies 5, 9, 13, 14, 16, 47, 49, 53 and 2 unlabeled colonies. The 11th female was out on the open sand between colonies. The area was checked twice in September and the beetles and ants were still active. Colonis 5, 9, 13 and 16 were active in 1959 but this record is the first for colonies 14, 47, 49 and 53.

On April 22, 1961 a *C. stathamae* was found being taken toward a nest by a single specimen of *M. mimicus* but their course was erratic because the ant was holding the beetle by the left front leg. The beetle was doing most of the propelling and being off balance much of the motion was circular. In 45 minutes they traveled about 20 feet and although they came within 6 or 8 inches of the nest several times the ant was not able to get the beetle in and finally deserted it. The beetle remained motionless for about 15 minutes and was then placed just inside the nest crater. Only 2 or 3 ants had been seen at the nest up to this time when 10 or 12 rushed out of the hole, siezed the beetle and disappeared into the nest. The beetle was not observed being ejected during the next hour.

In addition to these observations on *C. stathamae* Cazier the junior author took 2 old (badly rubbed) but live specimens of

C. constricticollis Cazier. One male was being taken into colony 32 by 3 ants at 10:55 A.M.

There are several other interesting side lights to the main study but these will require additional observation and laboratory work. On a number of occasions small bee flies, Bombyliidae, were seen hovering over the *M. mimicus* Wheeler nests, dipping down now and then over the hole and dropping the abdomen as if putting eggs into the ant burrow. When a jar of preserved material excavated from a *M. mimicus* Wheeler nest was examined a medium sized dipterous larva was present.

On September 11, 5 case bearing larvae were found at the entrances to the *M. mimicus* Wheeler burrows. Two were taken just inside the crater of the colonies, 1 was just coming out of the entrance, 1 was being dragged out of colony number 16 by 2 or 3 ants and the fifth was on the side of the crater with 2 ants trying unsuccessfuly to dislodge him. Three specimens were collected for rearing but as yet are still in the larval stage. They are probably the case bearing larvae of the Chrysomelid genus *Saxinus* and if so they may be the larvae of any one of about 6 species recorded from Arizona.

Summary

1. Myrmecophilous scarab beetles in the tribe Cremastocheilini from North America have been found associated with ants belonging to 11 genera.
2. The true relationship between members of the genus *Cremastocheilus* and its ant hosts is undetermined.
3. It is suspected that different species in this genus are at various stages in the evolution toward complete symbiosis with the ants.
4. *Cremastocheilus stathamae* Cazier at a location 7.5 miles from the Southwestern Research Station is a willing guest of the honey ant *Myrmecocystis mimicus* Wheeler.
5. This ant assists the beetle into the nest and then for some undetermined reason expels it. This may occur within minutes or days and possibly months after its entrance into the nest.
6. During several summer months *M. mimicus* Wheeler brings animal booty into the nest almost exclusively. In October and November they also bring in nectar and possibly honeydew presumably for winter storage in the repletes.

7. *C. stathamae* Cazier is not confined to a single an colony and travels for considerable distances. It is also associated with the ant *Novomessor cockerelli* (E. Andrea).
8. *C. constricticollis* Cazier and *C. lengi* Cazier are also guests of *M. mimicus* Wheeler.

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ENTOMOLOGISTS ON THE MOVE

Professor A. H. MacAndrews, a forest entomologist of note, has retired as Chairman of the Department of Forest Entomology at Syracuse University. With Boulder, Colorado as his new address, he plans to cooperate with the federal and state agencies on a special Black Hills Bark Beetle control project. It is also his intention, now that he has ''retired,'' to begin a collection of Colorado forest insects of importance.

Dr. Mont A. Cazier, formerly Resident Director of the Southwestern Research Station of the American Museum of Natural History, Portal Arizona is now associated with the Department of Entomology and Parasitology of the University of California at Berkeley.